

The Influence of Traction on the Formation of Mechanical Tissue in the Stems of Plants

BY
JOHN SERENUS BORDNER, A.B.
FERRY FELLOW IN BOTANY

A THESIS

SUBMITTED TO THE FACULTY OF THE DEPARTMENT OF LITERATURE,
SCIENCE, AND THE ARTS OF THE UNIVERSITY OF MICHIGAN,
IN CANDIDACY FOR THE DEGREE OF DOCTOR OF
PHILOSOPHY, IN JUNE, 1908

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THE INFLUENCE OF TRACTION ON THE FORMATION OF MECHANICAL TISSUE IN STEMS¹

JOHN S. BORDNER

Introduction

The following investigation was directed to a further knowledge of the influence of traction in the direction of the longitudinal axis on the formation of mechanical tissue in the stems of plants.

Petioles, tendrils, and roots were not investigated, because the work of HEGLER (9), BALL (1), and HIBBARD (11) was primarily on stems, and it was my purpose to add further and more detailed experimental evidence to the work done by these investigators.

This research was carried on in the Botanical Laboratory of the University of Michigan. It was under the direction of Prof. F. C. NEWCOMBE, to whom I am indebted for encouragement and helpful suggestions. I wish, also, to express my appreciation of the interest manifested in my work by the other members of the staff in the botanical department.

Historical

I. STEMS: INFLUENCE OF TRACTION

BARANETSKY (2) observed that a stem of *Gesneria tubiflora* weighted with 30^{gm} made less growth than one remaining free. SCHOLTZ (26) verified this observation of BARANETSKY, and found that stems when subjected to traction first grew more slowly and later more rapidly than the control plants. This he attributed to a change in the physical condition of the cell resulting from the reduced hydrostatic pressure. He furnished no experimental evidence to support his theory. HEGLER (9) produced the first experimental evidence to show that plants respond to tension by an increased formation of mechanical tissue. This supported the theory which was generally adhered to by plant physiologists previous to that time; viz., that a plant reacts to a gradually increasing strain by an increased

¹ Contribution No. 111 from the Botanical Department of the University of Michigan.

development of its mechanical tissue. In reporting the work of HEGLER, PFEFFER (21) says that a seedling of *Helianthus annuus*, whose original breaking strength was 160^{gm}, had a breaking strength of 250^{gm} after two days under the pull of 150^{gm}. No breaking strength is given for a control. A petiole of *Helleborus niger* which withstood a weight of only 400^{gm}, PFEFFER reports to have held a weight of 3.5^{kg} after 5 days, during which time it had been weighted with a gradually increasing load, while similar petioles under normal conditions gained but little in strength. Changes are also reported in the anatomical structure: (1) an increase in the number of cells of the collenchyma, (2) an increased thickness of the walls of the collenchyma, sclerenchyma, and bast, and (3) the production of entirely new tissues. It is unfortunate that a full account of HEGLER's methods and work was not published.

HEGLER (10) showed that the phenomenon observed by BARANETSKY and SCHOLTZ was not purely physical, but that a physiological change took place within the cell, due to stimulation coming from the tension. As evidence, he demonstrated that when plants were deprived of oxygen or when they were under the influence of chloroform, there was no response. He also found that the plants under tension were more turgid than controls, instead of less as SCHOLTZ had claimed.

RICHTER (25) concluded that when the stems of *Chara* were subjected to a longitudinal pull, there was an increase in strength. BALL's criticism of RICHTER's work is well taken. He says: "Die Resultate RICHTER's sind etwas zweifelhaft, da er keinen Vergleich zwischen belasteten *Chara* Pflanzen und unbelasteten von demselben Alter und derselben Grösse gegeben hat."

KÜSTER (15) found no response, and showed that in the petioles of *Helleborus niger* the new elements, which HEGLER (91) claimed were produced in response to tension, were there before tension was applied. PFEFFER (22, p. 148) also found no response in the production of mechanical tissue in plants subjected to tension.

VÖCHTING (27) investigated the influence of tension on sunflowers and cabbages that had been prevented from flowering by means of decapitation. He found that no new tissue was formed, and that no increase in mechanical tissue occurred as a result of tension.

WIDERSHEIM (29) experimented with pendant branches of *Fraxinus*, *Fagus*, *Caragana*, *Sorbus*, *Ulmus*, and *Corylus*. He fastened weights directly to these branches and continued the experiment through most of the growing season. Only in the case of *Corylus* was there any response; viz., an increase in the number of bast fibers.

BALL (1) experimented with *Helianthus annuus*, *Phaseolus multiflorus*, *Lupinus albus*, *Helleborus niger*, *Ricinus communis*, two species of *Cyperus*, and *Mirabilis jalapa*. His conclusion was that these plants do not respond to tension by an increase of their breaking strength or by the production of mechanical tissue.

HIBBARD (11) found an increase of mechanical tissue in the stem of *Vinca major* when the same was subjected to longitudinal pull. He failed to find any response in the stems of *Helianthus annuus*, *Ricinus communis*, *Brassica oleracea*, and *Phaseolus multiflorus*. HIBBARD did not determine the breaking strength of his stems.

2. STEMS: THE INFLUENCE OF COMPRESSION; ALSO COMPRESSION AND PULL COMBINED

KNIGHT (14) tied a young tree in such a manner that it was swayed only in the plane of the prevailing wind. After the lapse of one growing season, the diameter in this plane was found to be greater than the diameter at right angles to the same.

HIBBARD (11) found that compression caused a small increase of mechanical tissue in the stems of *Fuchsia*, *Vinca*, and *Helianthus*, while *Coleus* gave no response.

3. ROOTS: RESPONSE TO TENSION

HIBBARD (11) says: "Pull in the direction of the longitudinal axis of the plant called forth a small increase of mechanical tissue in the main and lateral roots of *Helianthus annuus* and *Ricinus communis*."

4. TENDRILS AND PETIOLES

DARWIN (4; GRAY 8, p. 176) says that in the grape-vine, Virginia creeper, etc., attached tendrils thicken and harden, gaining wonderfully in strength and durability, while those which remain unattached soon shrink up or wither and fall off.

MÜLLER (18) found that contact produced earlier and greater lignification of the sclerenchyma, even in the free portion of the ten-

drils of the Cucurbitaceae; but he did not consider tension as a probable factor along with contact.

WORGITZKY (30) reports that tendrils of *Passiflora quadrangularis* which had grasped a support broke at 600^{gm}, while the controls broke at 350^{gm}. With tendrils of Cucurbitaceae, the uncoiling resistance was thirteen times as great in those which had grasped a support. There was also a marked anatomical change; viz., a lignification of the pith parenchyma, which he assigned to no cause.

VON DERSCHAU (28) found that a gradually increasing pull on certain twining petioles raised their breaking strength and caused an increased development of mechanical tissue. He found a numerical increase in almost all kinds of cells. The petioles of *Solanum jasminoides* showed the least response.

NEWCOMBE (19, p. 446) says, in speaking of the reaction of tendrils to contact: "The first strengthening tissue is here laid down as a response to contact; its increase is the regulatory response of the plant to the strain that it feels."

MACDOUGAL (17, pp. 377, 378) believes that contact stimuli are not transmitted beyond 2 or 3^{mm}. Since the thickening of the tendril always takes place after contact, the natural conclusion would be that this thickening of the tendril is due to the traction exerted by the weight of the stem supported by it.

PEIRCE also (20, p. 241) believes that the strengthening of the free basal portion is not due to contact.

FITTING (6, p. 476) has demonstrated that contact stimuli are transmitted to the basal portion of the tendril, and that therefore the effect of contact stimuli on the basal portion of tendrils cannot be excluded.

5. CORRELATION

The factor of correlation has been investigated by numerous workers. Since self-regulatory development may imply a certain degree of correlation, it seems desirable that at least a brief review of the work on correlation should be given.

LABORIE (16) found decided differences in the anatomical structure of the floral axis compared with the rest of the plant: (1) an increase of bast, (2) a decided modification of the main bundles, and (3) a decrease of pith.

KLEIN (13) found the bundles more centrally located in the fruit stalk than in the petiole. He attributed this arrangement to the necessity for a greater mechanical strength, as well as for a more abundant supply of building material.

DENNERT (5) compared the anatomical structure of the fruit stalk before and after the ripening of the fruit. He found an increase in the development of mechanical tissue. There was an increased amount of xylem and a greater thickness of the walls of the wood fibers.

REICHE (24) investigated the transformation from flower to fruit stalk in many additional plants. His conclusions agree with those of the earlier investigators.

PIETERS (23) showed that one-year-old fruit-bearing shoots of the apple and the pear had a smaller xylem cylinder in proportion to their diameters than the vegetative shoots of same age. They were well supplied with supplementary mechanical tissue, however, which was distributed at those points where it was most needed. In the case of the peach and the plum, the woody cylinder of the fruit-bearing shoot was larger than in the vegetative shoot. There was an abundance of well-lignified sclerenchyma and hard bast in the fruit-bearing shoots of the apple and pear, while in the vegetative shoots these tissues appeared only sparingly, if at all.

GOEBEL (7, p. 206) writes: "Careful research demonstrates the existence of reciprocity between parts of the plant body. . . . The size and construction of one organ are frequently determined by those of another."

BOODLE (3) states that the walls of the sieve tubes and companion cells in *Helianthus annuus* become lignified as a result of strain. He also found a slight lignification of the parenchymatous parts of the pericycle and medullary rays, thus uniting the primary sclerenchyma strands into a more definite mechanical system attached to the strong xylem by the medullary rays. He says: "This must give greater rigidity, which no doubt is required by the heavy fruiting capitula borne by the plants."

KELLER (12) reached conclusions directly opposed to those reached by BOODLE. He showed that a strong or light pull in the direction of the longitudinal axis of orthotropic flower stalks exerted

no influence on the development of mechanical tissue. The displacement of orthotropic flower shoots to a plagiotropic position, he claimed, caused a certain anatomical change. This he attributed to the change in position and not to tension. His conclusion does not agree with those of other investigators, viz., that mechanical development of the fruit stalk goes hand in hand with the development of the fruit.

Methods

In both greenhouse and field culture a much larger number of plants were grown than were used in each experiment. At the beginning of each experiment the strongest plants and those most nearly equal in size were selected, and the others were removed. This was done to reduce the chances, as far as possible, of individual variation.

In the greenhouse cultures, the pots with the plants were placed in a row. The plants were then measured and every other one was taken as a control. At the close of the experiment, an average was taken of all the data on the control, and also the experimental plants in each series. This was the method used by SCHOLTZ. By preliminary experiments, the writer was convinced that it was by far the most satisfactory, on account of individual variations in plants which make it very difficult to select any one plant that will be a fair control throughout the experiment for any one experimental plant.

The methods of BALL and HIBBARD for applying tension by pull in the direction of the longitudinal axis of the stem were followed. The writer was soon convinced, however, that for plants as large as those used in his experiments, the leather noose used by BALL as a tension fastening was not needed. Heavy cotton flannel and ordinary cotton cord, therefore, were used for this purpose in all these experiments. A strip of heavy cotton flannel 2.5^{cm} wide was wrapped at least twice around the stem. Over this, two cords were passed from opposite sides and back again. Each cord, thus passing twice around the stem, was drawn tight enough to keep the fastening from slipping. The ends of each cord were then tied to a second. These were united into one strand some distance above the fastening. This double cord was passed over a light running pulley, supported directly above the plant, and a weight was attached to its free end. A thin

strip of wood or bamboo about 10^{cm} long was placed crosswise between the cords coming up on opposite sides of the stem, to keep them from injuring the young leaves and growing tip of the stem.

In the field cultures, exactly the same methods were followed, except that the seeds were planted in rows. The inferior seedlings were removed, and only the stronger ones were left for experimental use. In most cases the heavy clay loam was sufficiently firm to keep the plants from being pulled up by the tension. In the few cases when the soil was not firm enough, heavy flat weights were used to hold it in place.

METHODS IN FINAL DETERMINATIONS

Method 1.—In all but two experiments the stems were tested by direct pull along their longitudinal axes to determine whether they had responded in a self-regulatory manner to traction by increasing their breaking strength.

Preliminary experiments convinced the writer that the method of obtaining the breaking strength used by BALL was not satisfactory, since too many of the experimental plants broke at or just below the tension fastening. Larger plants therefore were used. These were broken at some distance below the tension fastening, thus eliminating the unquestionably weakening effect coming from the pressure of a tension fastening on the young and tender stem.

For this purpose, a strong wooden frame was constructed, about 120^{cm} long and 50^{cm} high. Through the middle of the frame ran a shelf parallel with top and bottom. On this shelf rested the plant, blocks, and spring balance used in determining the tensile strength. To grasp the ends of the stem, 4 blocks of wood were selected, each being 5^{cm} thick, 10^{cm} wide, and 20^{cm} long. These blocks were laid together in pairs, one block above its mate, and grooves considerably larger than the stems were cut in the contact faces of each pair to receive the plant stem.

During the preliminary experiments, the stems, except in the portion to be tested, were wrapped in moist cotton and then imbedded in a damp mixture of sand and Portland cement. This mixture was placed in the groove of the lower half of the pair of blocks. The stem was then placed in position and more concrete was piled on top.

This was pressed down and around the stem by tightening the bolts which were used to draw the two blocks together. This method was satisfactory. It was soon found, however, that the stem could be held sufficiently firm by substituting moist cotton for the mixture of sand and Portland cement. Moist cotton, therefore, was used in all the experiments as packing to fasten the stem in the blocks.

When the stems were fastened in the blocks, one pair of blocks was hooked to the spring balance, and the other pair was secured to one end of the wooden frame. The spring balance was hooked in turn to an iron rod passing through the opposite upright of the wooden frame. On the end of this rod, protruding beyond the frame, was a large tail-nut. By turning this tail-nut with the hand, tension was brought on the spring balance, and through the balance on the plant stem. The breaking strength was read from the face of the spring balance.

After the stems were broken they were preserved either in 50 per cent. alcohol, or short sections were cut from just below the breaking point in the stems, and these were killed and fixed in 1 per cent. chrom-acetic acid, thoroughly washed, dehydrated in alcohol, and kept for future study.

The following methods were used in making microscopic examinations and measurements of the xylem and hard bast in the stems.

Method 2.—Measurements of the thickness of cell walls in stained free-hand sections, and also in some cases of microtome sections, were made by using an ocular micrometer. The results recorded are in each case an average of eight measurements taken in as many distinct areas of the cross-section.

Method 3.—The total xylem and hard bast areas were measured in some of the experiments by projecting a cross-section of the stem upon a bristol-board screen, and measuring the areas with a polar planimeter.

Method 4.—Camera lucida drawings of the total xylem and hard bast areas and also of the hard bast elements were made upon standardized bristol-board. The drawings were very carefully cut out with a sharp and pointed scalpel, and then weighed on a chemical balance. The number of hard bast elements were also counted by fastening the drawings of the hard bast elements over sheets of yellow

paper and checking off each element by marking through the lumen on the yellow paper underneath.

Method 5.—The hard bast elements were drawn by means of a camera lucida and then counted to determine whether an increase had resulted in response to the pull.

Method 6.—Radial and tangential microtome sections of acid-fixed material were made to determine whether any fibrous parenchyma existed directly around the hard bast areas. This method was used only on control stems of *Helianthus annuus*. It was the purpose to determine whether the elements which produced the increased number of bast fibers were present before the tension was applied and therefore only developed, or whether they were formed *de novo* in response to tension.

The plants investigated were *Helianthus annuus*, *Phaseolus vulgaris*, *Ricinus communis*, *Sinapis alba*, *Vicia Faba*, *Lupinus albus*, *Rubus occidentalis*, and *Vinca major*.

Experiments

Experiment 1. Helianthus annuus, greenhouse culture.—Ten vigorous plants were selected from a number of seedlings grown in pots 20^{cm} in diameter. The experiment began November 21, 1906, when they were mostly 10 to 15^{cm} in height, and ended 29 days later. The tension fastening was placed on the experimental plants just below the second pair of leaves. The controls were not supported. The pull applied to the experimental plants was gradually increased from 25^{gm} at the start to 300^{gm} on December 14, 1906. The slow growth of these plants may be due to the fact that during the entire experimental period there were only a few sunny days, and also to the shortness of the day at this season of the year.

Table I gives all the data from this experiment, except the following: By method 6, fibrous parenchyma was found in the control stems as a transitional form between the thick-walled hard bast fibers and the short-celled parenchymatous tissue. These longitudinal sections were taken from just above the cotyledons. The increased number of bast fibers in the experimental plants, therefore, may be accounted for as the result of the response of these fibrous cells to tension, which thus develop into hard bast fibers.

The actual area of the cell walls of the hard bast elements and their number was found by method 4, and the total xylem area by method 3.

TABLE I.—*Helianthus annuus*

No. OF PLANT	NOVEMBER 21		NOVEMBER 28		DECEMBER 14		DECEMBER 20		BREAKING STRENGTH IN GRAMS	CELL WALL AREA OF HARD BAST ELEMENTS IN GRAMS	NO. OF HARD BAST FIBERS	XYLEM AREA IN SQ. CM. X 10
	Height in cm.	Diam. in mm.	Height in cm.	Diam. in mm.	Height in cm.	Diam. in mm.	Height in cm.	Diam. in mm.				
Exp.												
1.....	19.	4.	29.	4.	50.4	4.	59.2	4.2	7711	6.837	691	8.8
2.....	13.1	3.2	19.	3.2	34.	4.1	41.6	4.2	5443	7.014	811	6.6
3.....	10.6	3.5	19.	3.5	37.8	3.6	44.7	3.5	5216	6.430	840	4.1
4.....	11.8	3.1	20.7	3.2	35.3	3.6	44.1	3.9	4626	5.488	682	8.8
5.....	9.	2.	20.2	2.	36.5	3.	44.1	3.2	5443	5.666	581	5.2
Total	63.5	15.8	107.9	15.9	194.0	18.3	233.7	19.0	28749	31.435	3605	33.5
Av....	12.7	3.16	21.58	3.18	38.8	3.66	46.74	3.8	5749.8	6.287	721	6.7
Control												
1.....	15.2	3.	22.7	3.	42.8	4.1	52.9	4.3	5352	5.145	597	6.6
2.....	11.3	3.5	17.7	3.5	34.	3.8	42.8	4.	3039	6.420	706	4.3
3.....	11.8	2.5	19.	3.	34.	3.4	41.6	3.5	3719	5.372	657	5.9
4.....	11.3	3.2	18.3	3.2	34.	3.2	39.	3.5	2494	5.498	632	3.7
5.....	9.	2.2	12.1	2.2	23.3	3.2	30.	3.4	3629	4.679	656	3.3
Total	58.6	14.4	89.7	14.9	168.1	17.7	206.3	18.5	18233	27.114	3248	23.8
Av....	11.72	2.88	17.94	2.98	33.62	3.54	41.26	3.7	3647	5.423	641	4.76

The percentages of increase in the experimental plants over the controls are the following: breaking strength 57.6 per cent.; cross-section of walls of hard bast 16 per cent.; number of hard bast elements 12.5 per cent.; and xylem area 40 per cent.

TABLE II.—*Helianthus annuus*

No. of plant	Height in cm.							Height to 2d pair of leaves	Diam. just above 1st pair of leaves in mm.	Distance of break below 2d pair of leaves	Breaking strength in kg
	June 21	June 22	June 24	June 26	June 28	June 30	July 1				
Exp.											
Av....	7.5	8.6	12.6	16.3	19.4	23.8	26.6	10.4	4.1	7.26	16.535
Control											
Av....	7.03	8.2	11.3	14.3	17.3	21.5	24.3	9.2	4.1	7.43	13.799

Experiment 2. Helianthus annuus, field culture.—After the inferior plants had been removed, those used in this experiment stood 15 to 20^{cm} apart in the row. Every other plant was used as a control. The tension fastening was placed just below the second pair of leaves on the experimental plants. The control plants were left free. The experiment began June 21, 1907, and ended ten days later. A tension of 250^{gm} was applied to the experimental plants at the beginning of the experiment. This was increased to 750^{gm} the following day and to 1900^{gm} on June 25.

Table II gives an average of the measurements and the breaking strength of these plants. The average increase in breaking strength for the experimental plants over the controls was 2736^{gm} or 19.6 per cent.

The height measurements in this experiment confirm the work of SCHOLTZ and HEGLER ('93), showing a lessening of growth during the first 24 hours, followed by an increased growth for the next four days.

TABLE III.—*Helianthus annuus*

No. of plant	Height in cm.		Height to 4th pair of leaves		Diam. just above 1st pair of leaves in mm.		Diam. just above 2d pair of leaves in mm.		Distance of break above ground in cm	Breaking strength in kg.
	July 18	July 30	July 18	July 30	July 18	July 30	July 18	July 30		
Exp. Av.	36.07	89.6	32.33	44.6	9.4	15.95	7.58	13.39	12.3	69.99
Control Av.	38.01	90.5	34.6	45.08	9.64	16.03	7.69	14.37	13.9	66.12

Experiment 3. Helianthus annuus, field culture.—Much older and larger plants than those used in experiment 2 were put under tension July 18, 1908. This was gradually increased from 200^{gm} at the start to 1950^{gm} on July 27. The experiment ended July 30. It was the purpose in this experiment to determine whether the same tension would have the same influence on larger and older stems as on younger and less woody ones. The average increase in breaking strength as shown in table III in response to a tension of practically 1900^{gm} was 3.87^{kg}, while in experiment 2 the increase for a period of 10 days was 2.74^{kg}. The increase as a percentage of the average

breaking strength of the controls in this experiment, 5.8 per cent., was much less than in experiment 2, since the breaking strength was so much greater.

The tension fastenings were made just below the fourth pair of leaves. Similar fastenings were made on the control plants, and from these the plants were fastened to upright supports to keep them from being swayed by the wind.

Experiment 4. Sinapis alba, field culture.—These plants grew approximately 15^{cm} apart in the row. Every other plant was used as a control. The tension fastening was placed just below the seventh node above ground. Similar fastenings were placed on the control plants. From these fastenings, the plants were attached to strong cords, stretched one on each side of the row and parallel to it. A weight of 250^{gm} was attached to the experimental plants on July 16, 1907, and gradually increased to 1150^{gm} on July 24. The experiment ended two days later. The details of this experiment are given in table IV. The average increase of the breaking strength of the experimental over the control plants was 4.8^{kg} or 32 per cent.

The anatomical structure of these stems was determined by methods 2, 3, 4, and 5. Free-hand sections were made of all the stems about 5^{mm} below the point where they broke. These sections were stained in anilin safranin and mounted in glycerin. All the slides were then taken by a second party who labeled them with a secret label. The measurements given in table IV were then made, after which the second party gave me the key to the labels. The measurements of the experimental plants were now separated from those of the controls. An average of each set shows a decrease of 10 per cent. in the total xylem area and an increase in the thickness of the xylem cell walls of 5 per cent. The increase in hard bast in 5 stems which were selected wholly by chance was 52 per cent. The increase of hard bast elements in the same stems was 38 per cent.

The total xylem area for the five stems in which the hard bast determinations were made was also measured by method 4, with results that agreed within less than one-half of 1 per cent. with the measurements made by method 3.

The hard bast in the controls was lignified in all but a few stems, where it was only partly lignified. Stem 18 showed the least lignifi-

TABLE IV.—*Sinapis alba*

No. of plant	Height in cm.		Height to fastening in cm.		Diam. just above ground in mm.		Distance of break above ground in cm.		Breaking strength in kg.	Cell wall area of hard bast in grams		No. of hard bast elements	Xylem area in sq. cm. $\times 10$		Average thickness of xylem cell walls in microns
	July 16	July 26	July 16	July 26	July 16	July 26	July 16	July 26		July 26	July 26		July 26	July 26	
Exp.															
1.....	18.3	60.	15.	23.	6.85	9.25	16	26	28.09				15.88	2.812	2.812
2.....	25.	55.5	19.	21.5	5.1	7.3	13	13	16.76				6.99	2.625	2.625
3.....	22.	56.0	17.2	19.	5.	6.07	8	8	21.29				7.62	4.312	4.312
4.....	14.8	48.5	12.	16.	4.65	7.5	7	7	24.46				12.70	3.437	3.437
5.....	19.	53.5	14.	18.	5.1	7.15	12	12	11.79				9.84	2.500	2.500
6.....	23.5	60.	18.5	23.	5.95	8.8	13	13	21.74				8.67	2.562	2.562
7.....	20.5	57.	15.5	21.	7.2	9.35	13	13	12.23				8.89	2.812	2.812
8.....	24.	70.	20.	22.	7.4	9.9	16	16	16.76				10.70	2.562	2.562
9.....	26.4	72.	21.8	30.5	7.45	9.33	20	20	24.92	11.395	656		11.11	3.124	3.124
10.....	24.	68.	21.	31.	6.05	7.32	21	21	28.09	11.801	861		9.53	3.625	3.625
11.....	27.	69.	22.7	20.	5.85	8.3	16	16	22.20	7.061	561		10.70	3.375	3.375
12.....	27.5	67.	20.5	26.	6.55	8.65	14	14	32.62				8.89	4.625	4.625
13.....	27.	72.	21.	29.	5.75	7.65	12	12	16.76				9.84	3.687	3.687
14.....	24.7	62.	20.8	26.	6.45	8.1	15	15	17.21				12.70	3.375	3.375
15.....	27.5	62.	19.8	21.	5.4	5.77	12	12	17.21	5.938	578		3.18	3.037	3.037
16.....	26.3	68.	23.	26.	47.	6.75	7	7	25.82	4.598	526		7.94	2.875	2.875
17.....	25.8	59.	21.5	26.	4.6	5.2	15	15	11.33				5.40	2.625	2.625
18.....	28.3	67.	22.	25.	5.15	6.5	8	8	18.57				8.26	3.000	3.000
19.....	17.	46.	14.	19.	4.1	7.1	7	7	7.70				9.53	2.750	2.750
Total.....	593.0	1172.5	359.3	452.0	109.3	145.99	245.	245.	375.55	40.791	3182		178.37	59.720	59.720
Average.....	23.6	61.7	18.9	23.8	5.75	7.68	12.9	12.9	19.77	8.158	636		9.39	3.143	3.143

TABLE IV.—*Sinapis alba* (continued)

No. of plant	Height in cm.		Height to fastening in cm.		Diam. just above ground in mm.		Distance of break from ground in cm.		Breaking strength in kg.		Cell wall area in grams		No. of hard bast elements		Xylem area in sq. cm. X10		Average thickness of xylem cell walls in microns	
	July 16	July 26	July 16	July 26	July 16	July 26	July 26	July 26	July 26	July 26	July 26	July 26	July 26	July 26	July 26	July 26	July 26	July 26
Control																		
1.....	23.4	55.5	20.	24.	5.10	7.25	15.	15.41	15.41	15.41					7.30	3.187		
2.....	20.3	63.	20.5	24.5	6.10	8.90	7.	15.41	15.41	15.41					11.43	3.062		
3.....	17.2	50.	14.6	17.5	4.15	5.75	13.	9.97	9.97	9.97					3.81	2.562		
4.....	20.3	63.	15.4	19.5	5.60	7.70	12.	19.94	19.94	19.94					9.53	2.937		
5.....	18.8	58.	14.5	19.5	5.35	8.22	15.	19.94	19.94	19.94					12.70	3.062		
6.....	26.	60.	22.5	34.	8.00	10.62	19.	10.41	10.41	10.41					19.05	3.000		
7.....	22.7	64.	17.5	21.5	7.20	9.35	10.	11.79	11.79	11.79					16.51	2.562		
8.....	24.4	63.	19.5	22.	6.20	8.73	7.	11.33	11.33	11.33					7.62	3.000		
9.....	21.7	66.	16.3	22.	7.00	8.63	5.	15.86	15.86	15.86					10.80	3.002		
10.....	26.3	66.	22.3	33.5	7.15	10.30	10.	21.74	21.74	21.74					10.60	2.437		
11.....	21.9	58.	18.0	20.	5.15	6.10	8.	9.51	9.51	9.51					6.35	3.437		
12.....	28.5	70.	28.3	34.5	6.30	7.00	17.	19.03	19.03	19.03					8.25	2.875		
13.....	28.7	62.	21.4	24.	5.00	6.25	7.	13.13	13.13	13.13					6.35	4.002		
14.....	25.8	66.	21.5	28.	5.80	7.72	13.	16.76	16.76	16.76					11.43	3.375		
15.....	27.7	79.	21.5	24.	5.00	6.55	8.	12.68	12.68	12.68					6.67	3.125		
16.....	24.5	57.	20.5	24.	6.10	7.80	7.	17.21	17.21	17.21					11.43	2.500		
17.....	31.5	73.	25.0	27.	5.20	6.00	12.	25.86	25.86	25.86					6.03	3.062		
18.....	26.3	51.	21.8	23.	4.40	7.50	13.	5.54	5.54	5.54					8.89	2.500		
19.....	26.5	61.	22.5	24.	5.40	7.45	8.	14.50	14.50	14.50					13.07	3.500		
20.....	19.5	53.	16.3	20.	4.80	9.10	10.	13.59	13.59	13.59					13.27	2.501		
Total.....	488.0	1237.5	396.9	486.5	115.60	156.92	225.	298.60	298.60	298.60	26.697	2305	205.10	59.868				
Average.....	24.4	61.87	19.84	24.32	5.78	7.85	11.25	14.93	14.93	14.93	5.339	461	10.51	2.903				

cation among the controls. Stems 5, 7, 12, and 15 were all well lignified. The hard bast in approximately 10 per cent. of the experimental stems was completely lignified. In the five stems for which the hard bast determinations were made, only a few elements were lignified in 8 and 9, while in 16 lignification of the hard bast was almost complete.

Experiment 5. Phaseolus vulgaris, greenhouse culture.—The plants for this experiment were grown and selected in a like manner to those for experiment 1. The tension fastening was placed just below the second pair of leaves. The experiment began October 21 and ended November 8, 1907. The weight attached to the experimental plants, 400^{gm} at the beginning, was increased to 950^{gm} after five days, and to 1150^{gm} November 5. The controls were left unsupported.

TABLE V.—*Phaseolus vulgaris*

No. of plant	Height in cm.		Height to 2d pair of leaves in cm.		Diam. just above ground in mm.		Diam. just above cotyledons in mm.		Place where stem broke	Breaking strength in kg.	Bast area in sq. cm. $\times 125$	Xylem area in sq. cm. $\times 20$
	Oct. 21	Nov. 8	Oct. 21	Nov. 8	Oct. 21	Nov. 8	Oct. 21	Nov. 8				
Exp. Av.	13.5	25.	12.1	14.1	4.34	4.82	3.1	3.3		6.795	88.08	6.59
Control Av.	13.3	20.8	12.0	12.8	4.16	4.53	2.98	3.34		5.098	76.57	5.42

The average measurements and results of this experiment are given in table V. The breaking strength shows an increase in the experimental plants over the controls of 1.7^{kg}, or 33 per cent. Sections taken just below the breaks showed an increase of 15 per cent. in the area of hard bast, and 22 per cent. in the area of the xylem. These measurements were made by method 3. The hard bast and xylem were equally lignified in experimental and control plants.

Experiment 6. Phaseolus vulgaris, greenhouse culture.—These plants, when the experiment was started, were ten days older than those used in experiment 5. The experiment began December 7, 1907, and ended January 7, 1908, at which date most of the blossoms had already fallen from the plants and the leaves were beginning to lose their chlorophyll. A weight of 250^{gm} attached to the experi-

mental plants at the beginning of the experiment was gradually increased to 900^{gm} on December 20. It was the purpose of this experiment to determine, by prolonging the experimental period and growing the plants to maturity, whether the response in the earlier and actively growing period was continued to the end of the vegetative period. For this reason no additional weights were added after December 20. Both experimental and control plants broke with almost the same weight. The experimental plants were much more brittle and in most cases broke with a smooth, clear break, while the controls showed more of the elasticity and toughness which was characteristic of the stems in experiment 5.

Experiment 7. Phaseolus vulgaris, greenhouse culture.—After finding that response to tension, if any had occurred in experiment 6, was vitiated by permitting the plants to grow to maturity, experiment 5 was repeated, beginning March 5 and ending fourteen days later. The weights used, 200^{gm} at the beginning, were increased to 450^{gm} March 9 and to 700^{gm} four days later. The experimental plants showed an average increase in breaking strength of 3.32^{kg}, or 42.5 per cent. The number of hard bast elements was determined by method 5. The experimental plants showed an average increase of 167, or 14.9 per cent. The results of this experiment, therefore, agree with those of experiment 5. The tension fastening in this and also in experiment 6 was made at the same place as in experiment 5.

Experiment 8. Vinca major, greenhouse culture.—In selecting plants for this experiment those were taken which had young and actively growing shoots, uniform in general appearance and length. No measurements were taken at the beginning of the experiment, December 1, 1906. The experimental shoots were put under a tension of 50^{gm} at the beginning, which was gradually increased to 300^{gm} on December 21. The control plants were fastened to an upright support, but were not under tension.

The breaking strength was tested in the internode just below the fastening which was in an active growing condition in each plant when the experiment was started. The average shows an increase in the experimental plants of 649^{gm}, or 15.2 per cent.

Experiment 9. Vinca major, greenhouse culture.—It was the purpose of this experiment to determine whether internodes which

were no longer elongating would respond to tension by increasing their breaking strength. For this reason, shoots older and larger than those in experiment 8 were used. The controls were supported as in experiment 8. A weight of 200^{gm} attached to the experimental shoots on November 15, 1907, was increased to 400^{gm} on December 14. The experiment ended January 8, 1908.

The third instead of the last internode below the tension fastening was tested for its breaking strength. No elongation and in many cases no growth in diameter took place in this internode. An average of the breaking strengths shows no response to tension for an internode which is no longer actively growing.

TABLE VI.—*Vinca major*

RECORD A

No. of plant	Height in cm.		Height to node just above fastening in cm.		Diam. just below fastening in cm.		No. of node just above fastening	Distance of breaking point below fastening in cm.	Breaking strength in kg.	Thickness of xylem cell walls in microns	Weight of xylem area in grams	Thickness of hard bast fibers in microns	No. of hard bast fibers
	Jan. 9	Jan. 25	Jan. 9	Jan. 25	Jan. 9	Jan. 25							
Exp. Av. . . .	29.	41.4	25.6	27.3	2.11	2.22		8.25	4.53				
Control Av. . . .	32.	44.	28.4	20.6	2.00	2.20		8.75	4.24				

RECORD B

Exp.	Mar. 2		Mar. 2		Mar. 2				Mar. 2	Mar. 2	Mar. 2	Mar. 2	Mar. 2
	29.2	95.2	27.	29.1	2.05	2.38							
Av. . .	29.2	95.2	27.	29.1	2.05	2.38		15	8.22	5.77	.2777	7.42	1276
Control Av. . .	28.6	62	26.	28.5	2.1	2.32		12.1	6.97	5.09	.2140	6.56	1297

Experiment 10. Vinca major, greenhouse culture.—This experiment was in large measure a repetition of experiment 8. Tension fastenings were made on all the shoots. Just enough weight was attached to the control shoots to hold them erect. The experiment began January 9, 1908, with a weight of 250^{gm} attached to the experimental plants. This was increased to 450^{gm} eight days later, and to 900^{gm} January 25. The internode to which the tension fastening was attached was in each case actively elongating at the beginning of the

experiment. One-half of the shoots were removed and tested January 25, i. e., after 16 days and subjection to a maximum tension of 450^{gm} . Table VI, record A, gives an average of the results for this part of the experiment. The average breaking strength is slightly increased in the experimental shoots.

The remaining shoots were tested March 2, 1908. An average of breaking strengths as given in table VI, record B, shows an increase in favor of the experimental shoots of 1.25^{kg} or 18 per cent. A study of the anatomical structure of these stems was made by methods 2, 4, and 5. These determinations show an increase of 30 per cent. in the entire xylem area, an increase in xylem wall thickness of 13 per cent., and the same increase in the thickness of the walls of the hard bast fibers. A count of the hard bast fibers showed no increase in the number of these elements.

Experiment 11. Ricinus communis, field culture.—The method in this experiment was the same as in experiment 2. The tension fastening was placed just below the second pair of leaves. The control plants were not supported. The experiment began July 20 and ended August 1. A tension of 300^{gm} at the beginning was gradually raised to 2350^{gm} two days before the experiment ended.

TABLE VII.—*Ricinus communis*

No. of plant	Height in cm.		Height to 2d pair of leaves in cm.		Diam. at base in mm.		Diam. just above 1st pair of leaves in mm.		Breaking strength in kg.	Distance of break from ground in cm.	Xylem area in sq. cm. $\times 10$	Av. xylem cell wall thickness in microns
	July 20	Aug. 1	July 20	Aug. 1	July 20	Aug. 1	July 20	Aug. 1				
Exp. Av.	24.4	44.83	16.25	17.77	8.18	12.18	10.66	13.01	43.86	10.24	27.07	3.038
Control Av.	22.8	43.8	16.4	19.6	8.44	11.41	9.95	12.56	41.22	10.4	25.99	2.929

The average results, given in table VII, show 43.86^{kg} as the average breaking strength for the experimental plants and 41.22^{kg} for the controls, or 6.4 per cent. The increase is slightly greater than the final weight which was attached to the experimental plants. The average xylem wall thickness and total xylem area, as determined by methods 2 and 3, show an increase respectively of 0.1μ and 4 per cent.

The bast fibers were not well defined; many of them only very slightly thickened. It was therefore impossible to make an accurate count of their number.

Experiment 12. Rubus occidentalis, field culture.—On June 25, 1907, ten young stems were selected which in general appearance were equally vigorous. Tension fastenings were placed on five of these approximately 35^{cm} from the ground. The controls were left free. A weight of 2.25^{kg} at the beginning was increased to 4.5^{kg} on July 6, and to 9^{kg} 24 days later. The experiment ended September 30.

The decrease in height in the experimental plants was very marked. Growth in diameter was also less. The total bast and xylem areas were determined by method 3, giving an average increase in bast of 13.6 per cent. over the controls, but a decrease in xylem of 30 per cent. This decrease may be partly attributed to the reduced growth in diameter of the experimental plants.

Experiment 13. Vicia Faba, greenhouse culture.—The experimental plants were put under tension on October 24, 1907, the fastening being placed just below the fifth node. Since *Vicia Faba* grows very rapidly, it was thought possible that it might respond to a stronger tension than that applied to stems of other species of like cross-section and age. A weight of 450^{gm}, therefore, was applied at the beginning, increased to 900^{gm} two days later, and to 1300^{gm} on November 6. Since illumination is greatly reduced at this time of the year and growth is comparatively slow, this large weight caused the stem to elongate more rapidly than the control. This was accompanied by diminished growth in diameter. The control plants were left free, and since *Vicia Faba* retains its orthotropic position with great difficulty, these grew larger in diameter and less in height. When the experiment ended on November 9, the breaking strength of the experimental plants was less than the breaking strength of the controls.

Experiment 14. Vicia Faba, greenhouse culture.—The results of experiment 13 gave cause for this experiment, in which an effort was made to eliminate or at least minimize the effect of those factors which may have obscured the response to tension in the last experiment, if such a response did occur. For this reason, the experiment was carried on during the season of the year when illumination was much stronger and hence the chances for growth much better, all other

factors affecting growth remaining unchanged. Smaller weights also were used on the experimental plants, and the control plants were supported by small weights, barely sufficient to counterbalance the weight of plant, attached as the larger weights were to the experimental plants, the cords running over pulleys. The experimental and control plants were now growing under exactly the same conditions, except that the former were subject to tension of 200^{gm} at the beginning, increased to 450^{gm} on March 19, and to 700^{gm} on March 23, and finally to 950^{gm} on March 30. The experiment ended April 6.

TABLE VIII.—*Vicia Faba*

No. of plant	Height in cm.		Height to 4th node in cm.		Diam. just above 1st leaf in mm.		Diam. just below 4th node in mm.		Distance of breaking point above ground in cm.	Breaking strength in kg.	No. of hard bast fibers	Xylem area in sq. cm. $\times 18$
	Mar. 14	Apr. 6	Mar. 14	Apr. 6	Mar. 14	Apr. 6	Mar. 14	Apr. 6				
Exp. Av.	21.3	69.8	15.9	20.3	5.6	8.49	4.82	6.33	8.8	24.91	1630.3	22.75
Control Av.	22.4	66.	15.3	18.0	6.01	8.40	4.80	6.39	9.3	20.59	1419.4	21.00

The results are given in table VIII. The breaking strength shows an increase of 4.35^{kg} or 21 per cent. for the experimental plants over the controls. The number of hard bast fibers, determined by method 5, and the total xylem area by method 3, show an increase in the former of 14.8 per cent., and in the latter of 8.3 per cent.

TABLE IX.—*Lupinus albus*

No. of plant	Height in cm.		Height to cotyledons in cm.		Diam. half-way between ground and cotyledons in mm.		No. of hard bast fibers	Xylem area in grams
	Mar. 2	Mar. 30	Mar. 2	Mar. 30	Mar. 2	Mar. 30		
Exp. Av.	4.74	9.02	3.54	5.06	3.71	2.91	839.4	.9127
Control Av.	4.7	6.95	3.55	3.97	3.70	2.97	755	.800

Experiment 15. Lupinus albus, greenhouse culture.—This experiment began March 2 and ended March 30, the experimental plants

being subjected to a tension of 250^{gm} at the beginning, increased to 500^{gm} seven days later, and to 750^{gm} on March 19. On account of the shortness of the stems, which made it impossible to fasten them into the apparatus firmly enough to hold a sufficient weight, the attempt to determine the breaking strength of these stems was unsatisfactory. The reduced diameter, in that part of the stem below the cotyledons as shown in table IX, was due to a collapse of the tissue surrounding the stele. The total xylem area and number of hard bast elements, determined by methods 4 and 5, show an average increase of the former to be 14 per cent. and of the latter 11 per cent.

Summary

An average of the different determinations made in the foregoing experiments is given in table X. In all except experiment 9 with *Vinca major* and experiment 13 with *Vicia Faba*, the average breaking strength in the 246 tests shows an increase in the experimental plants over the controls. This must be attributed to a response to traction along the longitudinal axis of the stem. The negative results in experiment 9 show that the older part of the stem, where active growth has ceased, does not respond by increasing its breaking strength. The lack of response in experiment 13 with *Vicia Faba* can be attributed to factors which vitiated the influence of tension. These conditions are fully explained in experiments 13 and 14. Experiments 9 and 13, therefore, may be left out of consideration. The average area of the cell wall of the hard bast elements shows an increase in the experimental plants over the controls for *Helianthus annuus* and *Sinapis alba*. This determination was not made for the other species investigated. The average number of hard bast elements shows an increase in the experimental plants over the controls in all the species for which this determination was made, except *Vinca major*. *Phaseolus vulgaris* and *Rubus occidentalis* also show an increase of total bast area in the experimental plants over the controls. The average thickness of the hard bast fibers in *Vinca major* was found to be greater for the experimental stems.

In the total xylem area determinations, the only decrease was in *Sinapis alba* and *Rubus occidentalis*, in both of which, however, there

was an increase in hard bast. The other species all responded to tension by increasing their xylem area. The average thickness of

TABLE X.—SUMMARY

No. of experiment	Name of plant	Average breaking strength in kg.	Average cell wall area of hard bast fibers	Average no. of hard bast fibers	Average total hard bast area	Average thickness of hard bast cell walls	Average total xylem area	Average thickness of xylem cell walls	No. of stems used
Exp. 1...	<i>Helianthus annuus</i>	5.750	6.287	721			6.70		5
Cont. 1...	<i>Helianthus annuus</i>	3.647	5.423	641			4.76		5
Exp. 2...	<i>Helianthus annuus</i>	10.535							12
Cont. 2...	<i>Helianthus annuus</i>	13.799							13
Exp. 3...	<i>Helianthus annuus</i>	60.990							12
Cont. 3...	<i>Helianthus annuus</i>	66.120							11
Exp. 4...	<i>Sinapis alba</i>	19.770	8.158	636			9.39	3.143	19
Cont. 4...	<i>Sinapis alba</i>	14.930	5.339	461			10.51	2.993	20
Exp. 5...	<i>Phaseolus vulgaris</i>	6.795			88.08		6.59		4
Cont. 5...	<i>Phaseolus vulgaris</i>	5.008			76.57		5.42		4
Exp. 6...	<i>Phaseolus vulgaris</i>	5.850							11
Cont. 6...	<i>Phaseolus vulgaris</i>	5.570							13
Exp. 7...	<i>Phaseolus vulgaris</i>	10.135		1288					4
Cont. 7...	<i>Phaseolus vulgaris</i>	7.815		1121					4
Exp. 8...	<i>Vinca major</i>	5.993							5
Cont. 8...	<i>Vinca major</i>	4.254							4
Exp. 9...	<i>Vinca major*</i>	6.560							15
Cont. 9...	<i>Vinca major*</i>	6.790							15
Exp. 10B	<i>Vinca major</i>	8.220		1276		7.42	2777	5.77	4
Cont. 10B	<i>Vinca major</i>	6.970		1297		6.56	2141	5.09	4
Exp. 11...	<i>Ricinus communis</i>	43.860					27.07		12
Cont. 11...	<i>Ricinus communis</i>	41.220					25.99		12
Exp. 12...	<i>Rubus occidentalis</i>				0.167		1.216		5
Cont. 12...	<i>Rubus occidentalis</i>				0.147		1.762		5
Exp. 13...	<i>Vicia Faba*</i>	7.190							8
Cont. 13...	<i>Vicia Faba*</i>	8.090							7
Exp. 14...	<i>Vicia Faba</i>	24.910		1630			22.75		7
Cont. 14...	<i>Vicia Faba</i>	20.590		1419			21.00		8
Exp. 15...	<i>Lupinus albus</i>			839			9127		5
Cont. 15...	<i>Lupinus albus</i>			755			8000		6

* See experiments for explanations of negative results.

xylem cells walls in *Sinapis alba* and *Vinca major* was also greater in the experimental stems than the controls.

Conclusion

The results of the foregoing experiments have convinced the writer conclusively that actively growing stems of the herbaceous plants investigated and of *Vinca major* respond to traction along their longitudinal axes, by increasing their breaking strength; also by an increased development of bast or of xylem, and in most cases by an

increase of both these mechanical tissues. The experimental evidence for *Rubus occidentalis* was too limited to be conclusive. The stems were already too old and mature when the experiment was started. The writer is convinced, however, by this experiment with *Rubus occidentalis*, that the tension used by WIEDERSHEIM (29) on pendant woody branches was not sufficient to send a stimulus past the stimulus threshold.

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